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# BIOLOGICAL BULLETIN

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## THE HOMING OF THE BURROWING-BEES (ANTHOPHORIDÆ).

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### INTRODUCTION.

The researches about to be described were conducted for the purpose of determining how the burrowing bees compare with the ants and the mud-dauber wasps in their method of finding the way home. During most of the month of August, 1908, from five to ten hours a day were devoted to this study. This made it possible to conduct several series of experiments. Since all of the series led to similar conclusions, only two of them will be recorded. The majority of the experiments were conducted upon a species of *Melissodes* Latrl., many nests of which existed in an abandoned garden of the Haines Normal School.

### SERIES A. EXPERIMENTS ON MELISSODES.

These experiments were conducted in a deserted garden. Before beginning the experiments proper, numerous preliminary observations were made for the purpose of obtaining information that would be helpful in conducting and interpreting the experiments.

Bearing in mind Bohn's assertion that the flights of certain Lepidoptera are anemotropisms and phototropisms,<sup>1</sup> much attention was given to the flight of these bees.

When these anthophorids are busy at work, the flight is certainly neither an anemotropism nor a phototropism, for neither the movements nor the orientation of the body bear any constant relation to either the direction of the wind or to the rays of the sun.

<sup>1</sup> M. Bohn, "Observations sur les Papillons du Rivage de la Mer," *Bull. de l'Institut Général Psychologique*, 1907, pp. 285-300.

Observation soon informed me that each burrow was visited by bees at approximately regular intervals. Some of the nest-holes were visited by a bee about once in twenty minutes, other nests were visited more frequently. I soon discovered that where each interval between the visits was much less than twenty minutes, two or more bees occupied the burrow in common;<sup>1</sup> but that where the interval was twenty minutes or more, then only one bee was occupying the burrow. This enabled me to select, with a certainty, burrows that were occupied by only one bee.

The following series of experiments was performed upon a bee that occupied a burrow all to itself. The burrow was situated in a small barren spot and surrounded by a few blades of grass, which partially covered the opening. The heads of several stalks of grass overlapped the barren spot. The bee arrived at 9:35 A. M. and immediately entered the burrow. At 9:37 A. M., it departed again for the field, without stopping to explore the surroundings of the nest-opening.

#### EXPERIMENT I.

*While the bee was afield, a rectangular piece of white paper, 12 cm. by 8 cm., in the center of which was a hole 13 mm. in diameter, was so adjusted over the nest as to have the hole in the paper coincide with the opening of the burrow.*

At 9:55 A. M., the bee arrived with its burden of pollen. Instead of entering the nest, it circled around and around. It then hovered, momentarily, over the white rectangle and then described yet wider circles in the air. This behavior was repeated several times. At 9:57 A. M., two minutes after its return from the field, the bee entered the nest. On again departing for the field, at 10:00 A. M., the bee hovered a while above the paper that surrounded the nest; then, after making several turns of a helicoid curve, flew away.

<sup>1</sup> To determine how many bees were occupying a burrow, I would plug the opening and then observe it carefully for an hour or longer. The bees, on returning, would circle about the nest. After a while they would usually try to dig around the plug. By counting the bees that appeared and tarried it was easy to determine how many bees were occupying the burrow. When the required information had been obtained, the plug was removed.

## EXPERIMENT 2.

*The same conditions as in experiment one.*

At 10:20 A. M., the bee arrived from its trip, hovered for less than half a minute and then dropped into the nest. At 10:24 A. M., the bee departed, without stopping to explore the surroundings of the nest.

## EXPERIMENT 3.

*About four inches to the east of the nest opening, a hole was made in the ground. Over this hole was placed the piece of white paper, with the hole in the center, which was adjusted over the nest in experiment two. A piece of water-melon rind, with a thirteen mm. hole in the center, was so adjusted over the nest as to have the hole in the rind coincide with the opening of the burrow. One half of the rind was brown, the other half yellowish green; the line dividing these two colors bisected the hole in the center of the rind.*

At 10:47 A. M., the bee arrived with its burden of pollen. It hovered above the melon-rind for a moment, then circled about the place. At 10:48 A. M., after a search of one minute, the bee entered the nest. On leaving the nest at 10:59 A. M., the bee examined carefully the surroundings before departing.

## EXPERIMENT 4.

*While the bee was afield, the piece of water-melon rind was removed and a rectangular piece of white paper, eight cm. long and five cm. wide, was arched over the nest in such a way as to form a tent six cm. high, the east and west ends of which were open. The rectangular piece of white paper, with the hole in the center, which was left in the same position as in experiment three, was situated just in front of the eastern opening of the tent.*

When the bee arrived, at 11:15 A. M., it circled about for two minutes [until 11:17 A. M.] and then dropped into the hole over which the rectangular piece of paper, with the hole in its center, had been adjusted. It emerged at once and, after circling about for a short time, reentered the same hole. It emerged immediately. Finally, at 11:18 A. M., three minutes after arriving on the spot, the bee entered the tent, through the eastern opening, and dropped into the burrow. On emerging from the nest, at 11:31 A. M., the bee hovered a moment inside of the

tent. It then passed out of the east opening and hovered for a few seconds above the tent. Then, keeping close to the top of the grass, it flew about for a while in a sub-helicoidal curve and then flew away to the field.

#### EXPERIMENT 5.

*The same conditions as in experiment four.*

At high noon, the bee arrived at the southern end of the tent. After hovering but a moment, it flew around to the front and entered the tent through the eastern opening. It then right-about faced and dropped into the burrow. On leaving, at 12:08 P. M., it hovered a moment inside of the tent, then departed without further exploration.

#### EXPERIMENT 6.

*The same conditions as in experiments four and five.*

On arriving from the field, at 12:28 P. M., the bee flew immediately, over the top of the tent, to the eastern opening and then directly to the burrow. It did not turn about before entering the nest. At 12:34 P. M., it departed without exploring the surroundings; it did not even hover in the inside of the tent.

#### EXPERIMENT 7.

*The same conditions as in experiments four, five and six.*

At 12:52 P. M., the bee appeared at the eastern entrance to the tent. Immediately the bee entered the tent and alighted on the ground. At once it flew upward and dropped into the burrow. At 12:59 P. M., it departed, without exploring the surroundings.

#### EXPERIMENT 8.

*The rectangular piece of white paper, with a hole in its center, was left in the same position as in experiments five to seven inclusive; but the tent, over the nest opening, was so adjusted as to have its open ends face north and south.*

At 1:25 P. M., the bee arrived at the eastern end of the tent. It immediately flew around to the southern entrance of the tent and entered the burrow.

The above eight experiments were performed August 14, 1908. On the next day (August 15) the following five experiments were performed with the same individual.

## EXPERIMENT 9.

*The same conditions as in experiment eight. The apparatus had been left in position for twenty hours. Something had trampled the tent to the ground. It was readjusted to the proper height.*

At 9:34 A. M., August 15, the bee arrived, hovered but a moment, and then entered the tent, through the southern opening, and dropped immediately into the burrow.

## EXPERIMENT 10.

*While the bee was afield, several stalks of grass were removed from the west side of the tent; thus increasing the width of the barren patch that surrounded the burrow. The other conditions were the same as in experiment nine.*

At 9:54 A. M., the bee arrived from the field. It circled about fully a minute before entering the tent. It then passed through the northern opening and immediately dropped into the burrow. On departing, at 9:59 A. M., the bee did not stop to explore the surroundings.

## EXPERIMENT 11.

*The same conditions as in experiment ten.*

On arriving, at 10:18 A. M., the bee circled about for a moment and then, entering the tent through the southern opening, immediately dropped into the burrow. At 10:23 A. M., the bee departed, through the southern opening, without stopping to explore the surroundings.

## EXPERIMENT 12.

*While the bee was afield, the tent, with the open ends facing north and south, was placed two inches to the west of the nest-opening. A rectangular piece of black paper, 12 cm. long by 8 cm. wide, with a hole 13 mm. in diameter in its center, was so adjusted over the nest as to have the hole in its center coincide with the opening of the burrow. The rectangular piece of white paper, with the hole in its center, was left in the same position as in experiment eleven.*

At 11:16 A. M., the bee arrived from the field, hovered a few seconds above the black paper, then dropped into the nest. On leaving, at 10:51 A. M., it hovered a short while before departing.

## EXPERIMENT 13.

While the bee was afield, the rectangular piece of white paper was so adjusted over the nest as to have the hole in its center coincide with the opening of the burrow. The rectangular piece of black paper was placed in the position occupied by the white rectangle in experiment twelve. The tent was left in the same situation as in experiment twelve.

On arriving, at 11:16 A. M., the bee hovered above the white paper, over half a minute, before dropping into the burrow. On departing, at 11:23 A. M., it hovered quite a while, examining the surroundings.

## EXPERIMENT 14.

While the bee was afield, all accessories were removed from the neighborhood of the nest and the barren patch covered with a thin layer of freshly mown grass. Care was taken to leave the opening to the burrow uncovered.

The bee arrived from the field at 11:50 A. M. and began to fly about in a sub-helicoidal curve. The radii of this curve became, irregularly, longer and longer until the bee had reached a fence fifteen feet away. Then the bee approached the nest and flew about in curves, the radii of which became, irregularly, shorter and shorter. At 11:52 A. M., after a search of two minutes, the bee dropped into the nest.

## SERIES B.

The bee upon which this series of experiments was conducted was a much smaller insect than the *Melissodes* sp.? upon which the above experiments were performed. One of those tragedies, which are so common in the insect world, brought this bee's labors to a close before I was ready to capture it; hence it was impossible to determine the genus to which it belongs. I am not even sure whether it is a member of the Anthophoridæ or of the Andrenidæ. In this connection, however, the exact name is a matter of little weight; for, although there are generic, specific and individual peculiarities of behavior, yet the general habits of all the burrowing bees are so similar, that it would be illogical to suppose that the method of finding the way home was not essentially the same in all genera.

Several of the walks of Haines Normal School, Augusta, Ga., are separated from the adjacent flower beds by bricks inclined in such a manner as to form a serrated border of wedges of bricks ; each wedge being about two inches high and something over four inches wide at the base. One of these flower beds, which was quite sandy, contained, in its center, a patch of nasturtiums. About two feet from the bricks, and parallel to the border, there extended, throughout the bed, a narrow row of violets. The remainder of the bed was bare. In a barren spot in this bed, adjacent to an inverted tin cap of a coca-cola bottle, and within an inch of the northern face of one of the bricks that formed the serrated border, a burrowing-bee had excavated a burrow. The nest was discovered at nine A. M., August 8, 1908. The sun was shining brightly at the time ; but the nest, which was situated a little to the west of the southern wall of a large three-story brick building, was in the shadow. A gentle breeze was blowing from the south. At the time mentioned, the bee was busy collecting pollen and storing it in the burrow. The flowers from which it obtained its supply must have been quite remote, for it required about thirty minutes to make a trip.

For convenience, the brick before which the burrow was located was designated zero and bricks to the west of it  $W_1$ ,  $W_2$ ,  $W_3$ , etc., in regular succession. Likewise the bricks to the east were named  $E_1$ ,  $E_2$ ,  $E_3$ , etc.

The field from which the bee obtained its pollen was situated to the south of the school, and the burrow of the bee was located to the north of the brick border. On arriving from its forage, the bee would reach the brick border at, or near, brick  $W_{10}$ . It then would turn about so as to face the northern surface of the brick border. Then hovering at about an inch and a half from the ground and about the same distance from the bricks, the bee would sidle along. Usually its movement was toward the east ; but, occasionally, it would retrograde westward a short distance and then resume its eastward progress. On reaching the brick before which its nest was located, it would drop immediately into its burrow. After remaining in the burrow a few minutes, the bee would depart, without stopping to explore the surroundings. Several trips of the bee were observed carefully and in

each case the behavior was essentially the same. In its flight, neither the orientation of its body nor the direction of its movements bore any constant relation either to the direction of the wind or to the rays of the sun.

### EXPERIMENT I.

*While the bee was afield, with a stick of the same diameter as the burrow, I punched, in the ground in front of bricks  $W_1$  and  $E_1$ , holes which bore the same relation to each of those bricks that the burrow opening did to brick zero. The inverted tin cap of a coca-cola bottle was removed from its place beside the burrow and placed, in the same relative position, at the side of the hole which I had made in front of brick  $W_1$ .*

The bee, on returning from the field, arrived at brick  $W_{10}$ . It then turned around so as to face the northern surface of the brick border. Then hovering at about an inch and a half above the ground and at about the same distance from the border, it sidled along. Most of the time it moved towards the east; but, occasionally, it retrograded westward, for a short distance, and then resumed its eastward progress. On reaching brick  $W_1$ , it dropped, at once, into the hole which I had made. It emerged at once and continued its eastward course until it reached its burrow, which it entered. It tarried in the nest a few minutes, then departed, without stopping to explore the surroundings, for the pollen field. Evidently, a slight topographical change of the neighborhood of the nest caused the bee to enter a false burrow, which it discovered was not its own.

### EXPERIMENT II.

*While the bee was afield, I punched holes, similar to those described above, before bricks  $W_2$ ,  $W_3$ ,  $W_4$ ,  $W_5$ , and bricks  $E_2$ ,  $E_3$ ,  $E_4$ —one hole before each brick. For descriptive purposes, I shall call the holes before bricks  $W_1$ ,  $W_2$ ,  $W_3$ , etc., respectively  $L_1$ ,  $L_2$ ,  $L_3$ , etc., and those in front of bricks  $E_1$ ,  $E_2$ ,  $E_3$ , etc.,  $R_1$ ,  $R_2$ ,  $R_3$ , etc.*

On returning from the field, the bee arrived at brick  $W_{10}$ . It then turned about so as to face the northern surface of the border, and, hovering and sidling, in the manner described in experiment I., it moved eastward until it reached hole  $R_1$ , into which it

dropped. Emerging at once, it hovered a moment and then dropped into the same hole. Again emerging it moved westward and dropped into its burrow. On emerging from the nest, it went immediately afield.

### EXPERIMENT III.

*While the bee was afield, I placed, before each of the holes I had made, except holes  $R_3$  and  $R_4$ , an inverted tin cap of a coca-cola bottle. The other conditions were the same as in experiment II.*

On returning from the field, the bee arrived at brick  $W_9$ . It turned about so as to face the northern surface of the border, and, in the hovering and sidling manner mentioned above, moved eastward, hovering momentarily over holes  $L_4$ ,  $L_3$ ,  $L_2$ ,  $L_1$ , until it reached the nest, which it entered immediately. There it tarried a moment, then departed, without stopping to examine the surroundings, for the pollen-fields.

### EXPERIMENT IV.

*While the bee was afield, I placed a small tent of white paper over the burrow. The tent, the whole north end of which was open, was three inches wide, at the base, two inches high and three inches long. The other conditions were the same as in experiment III.*

On returning from the field, the bee arrived at brick  $W_8$ . It then turned about so as to face the northern surface of the border and then, in the hovering and sidling manner mentioned above, it moved along, hovering, in the order mentioned, above holes  $L_4$ ,  $L_3$ ,  $L_2$ ,  $L_1$ . On reaching the tent, it retraced its steps, hovering over holes  $L_1$ ,  $L_2$ ,  $L_3$ ,  $L_4$ . It then resumed its eastward journey. Although it had been sometime since the bee returned from the field, yet it had not entered any hole. At this stage, however, it dropped into hole  $R_1$ . Emerging, it hovered a moment and then reentered the same hole. Emerging from the hole, it began to fly about in a random manner. Evidently it could not locate the burrow. It had passed over the tent several times, but had made no attempt to enter it.

*I now removed the tent, thus leaving everything in the same condition as in experiment III.*

In a few moments the bee reached the nest and, after hovering

a moment, entered. On departing for the field, it spent considerable time hovering about the burrow, as though it were examining the surroundings.

#### EXPERIMENT V.

*While the bee was afield, a rectangular piece of paper, 12 cm. long by 8 cm. wide, in the center of which was a hole 13 mm. in diameter, was so adjusted over the nest as to have the hole in the paper coincide with the burrow-opening. The other conditions were the same as in experiment three.*

On returning from the field, the bee arrived at brick  $W_{12}$  and turned about so as to face the northern surface of the border. In the hovering, halting, manner mentioned above, it sidled eastward, hovering a moment over each hole reached, but entering none. Over the nest it hovered a little longer than it did over holes  $L_4, L_3, L_2, L_1$ ; but, instead of entering, it continued its search eastward. On reaching hole  $R_1$  the bee dropped into it. Immediately it emerged, hovered a moment, then dropped again into the same hole. Reëmerging from hole  $R_1$ , it journeyed eastward and dropped into hole  $R_2$ . Emerging from this hole, it passed to brick zero, hovered for about a minute above the burrow but did not enter. It now began to roam about at random. After the lapse of some time, it reappeared above the nest, hovered a moment and then dropped into the burrow. On emerging from the nest, the bee hovered about for some time and then circled about the neighborhood, before departing for the field.

#### EXPERIMENT VI.

*The same conditions as in experiment V.*

On returning from the field, the bee arrived at brick  $W_{10}$ . In the hovering, halting, manner described above, it sidled eastward, halting over each hole, but entering none. It started to enter hole  $L_1$ , but retreated before the body was three fourths hidden. As soon as the nest was reached, the burrow was entered.

#### CONCLUSIONS.

It is evident that the behavior exhibited by the above experiments cannot be classed as either anemotropisms or as phototropisms, for neither the orientation of the body nor the direction

of flight bore any constant relation either to the direction of the wind or to the rays of the sun. Many of the nests observed by me were in the sunshine a part of the day and in shadow the balance of the day, yet the bee found the nest just as readily when it was in the shadow as it did when it was in bright sunlight.

Any pronounced change made in the topography of the vicinity of the nest, while the bee is away from its burrow, is sure to cause the insect, on its return, to be forced to search about in order to find the entrance to its home [Ex. 1, 3, 4, 10, 14, I., II., IV., V.]. This is true even when the nest opening is in full view [Ex. 1, 3, I., II.]. If the proper alterations are made in the topography of the vicinity of the nest, the bee may be induced to enter, temporarily, a false burrow [Ex. 4, I., II., IV., V.]. A bee that has not been experimented upon is much more affected by slight alterations made in the topography of the vicinity of the burrow than is the same bee after a prolonged period of experimentation [cf. Ex. 1 with Ex. 13 and 14]. All of these statements militate against the old idea of a "homing instinct," against Pieron's kinesthetic reflex hypothesis and against Bethe's contention that bees are guided home by an unknown force which acts reflexly; for if either of these assumptions were true, changes made in the topography of the vicinity of the nest should not alter the behavior of the bees.

It would be erroneous to claim that these burrowing-bees find their way home by the method of "trial and error," for there is no gradual "stamping in" of an appropriate response. When the bee, on returning home, finds the environment markedly changed, it searches until the opening of the burrow is found. Before departing again for the field, the bee makes a careful examination of the vicinity of the nest [Ex. 1, 3, 4, 13, IV., V.]. On its next return to the burrow, unless the environment has been changed in the meanwhile, the bee flies directly to the burrow in the minimal amount of time; there is none of that blundering into a solution which the method of "trial and error" demands [Ex. 2, 5, VI.].

By a process of elimination, the most consistent explanation of the above behavior is the assumption that burrowing-bees utilize memory in finding the way home, and that they examine

carefully the neighborhood of the nest, for the purpose of forming memory pictures of the topographical environment of the burrow. This assumption that the exploration of the vicinity of the nest is for the purpose of forming memory pictures is supported by the fact that such explorations are always made before beginning trips that immediately follow some pronounced change in the topography of the environment [Ex. I., 3, 4, 13, IV., V.], and not when such changes have not been made [Ex. 2, 5, 6, 7, 10, 11]. Slight changes in the topographical environment of the burrow may, at times, effectively disturb the bee on its homeward journey, and yet not be sufficiently pronounced to cause the departing bee to pause and reexplore the surroundings of the nest [Ex. I., II., III.].

HAINES NORMAL SCHOOL,  
AUGUSTA, GA., September, 1, 1908.